

Phenacomys albipes

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Phenacomys albipes Merriam, 1901

White-footed Vole

Phenacomys albipes Merriam, 1901:125. Type locality "Redwoods near Arcata, Humboldt Bay [Humboldt Co.], California."

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Arvicolinae, Genus *Phenacomys*, Subgenus *Paraphenacomys* (Carleton and Musser, 1984; Jones et al., 1992; Musser and Carleton, 1993; Repenning and Grady, 1988). Based on examination of two specimens, Taylor (1915) tentatively assigned *albipes* to the subgenus *Arborimus*, erected largely to separate *longicaudus* (red tree vole) from *intermedius* (heather vole) in the genus *Phenacomys*. Howell (1926:5) recommended against "recognition of a subgeneric division within the genus [because it] could be based only upon weakly defined characters, and that such a step would complicate, rather than clarify, our understanding of the subject." Johnson (1973:243) proposed elevation of the subgenus *Arborimus* to generic level for *longicaudus* because the number and diversity of differences equalled or exceeded those "currently accepted as valid at the generic level" among "microtine genera," a statement open to challenge at least for some subgenera within the genus *Microtus* (Hall, 1981). Johnson and Maser (1982) concluded, on morphological and ecological grounds, that *albipes* was allied more closely with *longicaudus* than with *Phenacomys intermedius*; they placed *albipes* with *longicaudus* in the genus *Arborimus*. Repenning and Grady (1988), on the basis of the shorter dentine tract (enamel-free area) on the buccal salient angle of the posterior loop of m1, indicated that assignment of *albipes* or its lineage to either the subgenus *Phenacomys* or *Arborimus* was inappropriate. Within the genus *Phenacomys*, they erected a new subgenus (*Paraphenacomys*) for *albipes* and two fossil species (*brachyodus* and *gryci*) and retained the subgenus *Phenacomys* for *intermedius* and a fossil species (*deeringensis*) and the subgenus *Arborimus* for *longicaudus* and the then unnamed species *pomo* (Johnson and George, 1991). In recently published treatments, some workers have recognized elevation of *Arborimus* to generic level for *albipes*, *longicaudus*, and *pomo* (e.g., Musser and Carleton, 1993), but others have continued to use *Phenacomys* for *albipes* and *longicaudus* as well as for *intermedius* (e.g., Jones et al., 1992; McAllister and Hoffmann, 1988). We presume that the latter authors would have included *pomo* in *Phenacomys* with its sibling species *longicaudus* (Johnson and George, 1991). No subspecies of *P. albipes* are recognized currently (Hall, 1981).

DIAGNOSIS. *Phenacomys albipes* (Fig. 1) has been described as superficially resembling *Microtus longicaudus* (Howell, 1926) and *Clethrionomys californicus* (Taylor, 1915). It may be



FIG. 1. Photograph of adult female *Phenacomys albipes* from 1 mile south Summit, Benton Co., Oregon (KU [University of Kansas, Museum of Natural History] 145695).

separated from all other sympatric arvicolines by a combination of rich brownish-gray ("grizzled-bister"—Merriam, 1901:125) pelage, a tail >50 mm long and >50% of length of head and body, and light grayish or whitish feet. The genus *Phenacomys* can be separated from other arvicoline genera in the geographic range of *P. albipes* by reentrant angles on lower molars about twice as deep on the lingual as labial side (Fig. 2a). The skull of *P. albipes* is recognizable from those of congeners by a combination of relatively narrow incisive foramina, M3 with three loops of enamel on the lingual side, nasals that obscure the anterior faces of the moderately recurved incisors, and deep lateral pterygoid fossae (Fig. 3).

GENERAL CHARACTERS. *Phenacomys albipes* is a moderately large, *Microtus*-like vole with a slender, sharply bicolored, and scantily haired tail (Merriam, 1901); the white ventral stripe is wider than the dusky dorsal stripe (Fig. 1; Taylor, 1915). The ears are moderately large (11–13 mm) and scantily haired, sometimes nearly naked at the tip. The eyes are small. The hind feet usually are >19 mm long. The sacral foramina are large, the sternum is wide, and the acromion process of the scapula is narrow (Johnson and Maser, 1982). The skull (Fig. 3) is long and narrow, the septum between the nares slopes posteriorly, and the premaxilla-maxilla suture is at an angle of ca. 25° to the vertical axis of the skull. The

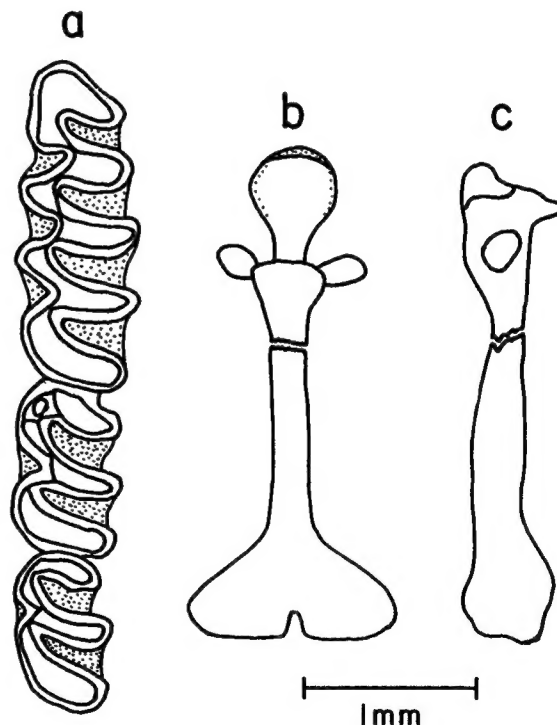


FIG. 2. a. Camera-lucida drawing of the occlusal surface of the left lower molars (anterior at top) of an adult male *Phenacomys albipes* (OSUFW [Oregon State University Department of Fisheries and Wildlife] 7360) from 6 miles W Blue River (T16S, R3E, Sec. 22), Lane Co., Oregon; b and c, camera-lucida drawings of dorsal and lateral views, respectively, of the baculum of an adult male *Phenacomys albipes* (PSM [James R. Slater Museum of Natural History, University of Puget Sound] 14526) from 4 miles SE Bandon (T29S, R14W, SW¼ Sec. 9), Coos Co., Oregon. The baculum was fractured, presumably after the animal was dead.

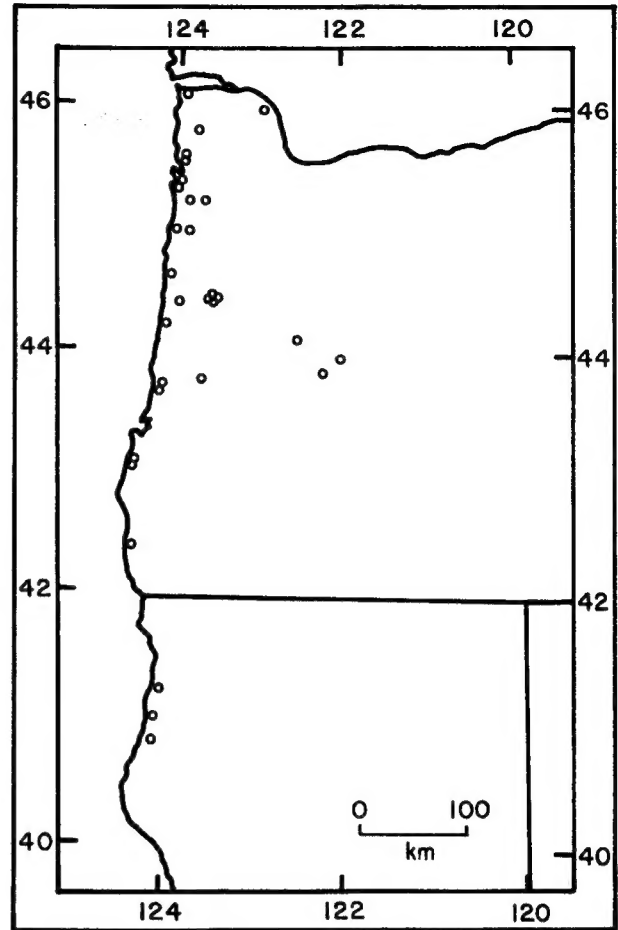


FIG. 4. Distribution of localities at which *Phenacomys albipes* reportedly was taken. Map redrawn after Maser and Johnson (1967) and Olterman and Verts (1972).

baculum (Figs. 2b, 2c) is atypical of those of most arvicolines in that a separate medial process is absent and the lateral processes frequently are fused. There are four, five, or six mammae (Johnson and Maser, 1982); Hall and Cockrum (1953) gave eight mammae as a generic character for *Phenacomys*, but within the genus seemingly this number is restricted to *P. intermedius* (Johnson and Maser, 1982).

The molars are rooted and lack cement (Kurtén and Anderson, 1980). Both M3 and m3 are wide and short, although the latter is longer than in *P. longicaudus*. On M3 the outer portion of the posterior crescent is closed off or narrowly open, forming a second outer triangle (Taylor, 1915). The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16.

Means and ranges (in parentheses) of external measurements and means of skull measurements (in mm) of males ($n = 6$) and females ($n = 5$) are (Howell, 1926): total length, 166 (158–176), 182 (170–187); length of tail, 67 (60–72), 73 (66–83); length of hind foot, 20 (19–21), 21 (21–22); condylobasal length, 21.9, 22.5; length of nasals, 7.2, 7.8; interorbital breadth, 3.5, 3.3; zygomatic breadth, 14.0, 14.2; lambdoidal width, 11.5, 11.9; length of incisive foramina, 4.6, 4.6; length of maxillary toothrow, 5.7, 5.8; and height of skull, 9.0, 9.4. The length of the diastema ranges from 6.5 to 7.2 mm (Johnson and Maser, 1982).

FIG. 3. Dorsal, ventral, and lateral views of the cranium and lateral and dorsal views of the mandible of adult male *Phenacomys albipes* (OSUFW 7360) from 6 miles W Blue River (T16S, R3E, Sec. 22), Lane Co., Oregon. Occipitonasal length is 25.73 mm.

DISTRIBUTION. *Phenacomys albipes* occurs from the Columbia River south through the Coast Range of Oregon to Arcata, Humboldt Co., California, and in Lane Co., Oregon, on the west slope of the Cascade Range, eastward to Vida (Fig. 4; Maser and Johnson, 1967). The species occurs from near sea level to 1,067 m in the Coast Range (Maser and Johnson, 1967).

FOSSIL RECORD. One fossil record of *P. albipes* is known, a $\pm 13,000$ -year-old m1 from the Smith Creek Cave fauna, White Pine Co., Nevada (Repenning and Grady, 1988) originally identified as *Phenacomys cf. intermedius* by Mead et al. (1982). The subgenus *Paraphenacomys* to which *P. albipes* is assigned "is known in North America from 2.4 million years ago to the present" (Repenning and Grady, 1988:9).

FORM AND FUNCTION. Individuals in which "the termination of the reentrant angle of the molars becomes visible beyond the level of the alveolus" are considered fully mature. Those in which the occlusal pattern had become worn and lost are considered senescent (Johnson and Maser, 1982:17).

The proximal flaps in the gastric mucous-membrane pouch have long, irregular, and deep serrations; the distal rim has small broad serrations. The cecal villi are delicate, but unlike those in *P. longicaudus*, a few are branched (Johnson and Maser, 1982).

The claws were considered by Maser et al. (1981:200) to be "more of a digging than a climbing type." This, combined with the small eyes, was considered indicative of a burrowing habit. Nevertheless, the species later was considered to be scansorial (Voth et al., 1983).

ONTOGENY AND REPRODUCTION. A pregnant female was taken in April and two were taken in July (Maser and Johnson, 1967); Maser et al. (1981) indicated that *P. albipes* bred throughout the year. Mean litter size ($n = 9$) averaged 3.0 (range, 2–4—Johnson and Maser, 1982). An adult female and a litter of three 2.4-g young were captured by hand in a nest on the ground (R. Hoyer, pers. comm., 7 June 1993). No other published information regarding reproduction is available and none is available concerning postnatal development.

ECOLOGY AND BEHAVIOR. Most of the early published information on habitats occupied by *P. albipes* is anecdotal. Specimens were caught under "a log-jam near the bank of a stream which flows through dense redwood and maple forest" (Howell, 1920:242); among "mossy stones along a small stream that flows through heavy forest of Douglas fir" (Jewett, 1920:167); in and under "a salmonberry thicket" (Jewett, 1920:167; Sherrell, 1969:39); in an area where "the climax forest tree is noble fir (*Abies nobilis*) with some western hemlock (*Tsuga heterophylla*)"; in "a steep sided canyon with some fallen logs, brushy forest and stream sides"; in "a grassy spot on a partly logged ridge top"; and "near a log, 15 feet above a moderately open spot, at the edge of a forest stream" (Maser and Johnson, 1967:25). Another was caught in the runway of a mountain beaver (*Aplodontia rufa*) in an area "covered by logs, . . . surrounded by dense vegetation, from which the following plants were identified: horsetail (*Equisetum* sp.); sword-fern (*Polystichum munitum*); deer-fern (*Struthiopteris spicant*); miner's lettuce (*Montia perfoliata*); nettle (*Lamium* sp.); foxglove (*Digitalis purpurea*); Canada thistle (*Cirsium arvense*); salmonberry (*Rubus spectabilis*); thimble-berry (*Rubus parviflorus*); vine maple (*Acer circinatum*); red alder (*Alnus oregona*)" (Maser and Johnson, 1967:26). Another specimen was caught in an early seral plant community resulting from the burning by wildfire of a 3-year-old clear-cutting 2 years earlier (Maser and Hooven, 1969). Many of these specimens were collected near small streams (Howell, 1920, 1928; Jewett, 1920; Maser and Johnson, 1967; Sherrell, 1969; Sturges, 1955; Walker, 1928) causing Maser and Johnson (1967:26) to suggest that the species was "associated with small streams." Maser et al. (1981) and Voth et al. (1983) classified the habitat of *P. albipes* as the riparian alder/small stream union. Nevertheless, some specimens were taken ≥ 100 m from streambanks (Maser and Hooven, 1969; Maser and Johnson, 1967; Voth et al., 1983).

Recent comparisons of small-mammal abundance in a variety of habitats have revealed that *P. albipes* in both Coast and Cascade ranges is associated with much of the forest sere (Anthony et al., 1987; Gomez, 1992; McComb et al., 1993). In a triple-replicated study of the comparison of abundance in 5–10 year old conifer-shrub, 20–35 year old sapling-pole conifer, sawtimber (110–200

year old) conifer forest, oldgrowth (200+ year old) conifer forest, and deciduous forest in the Coast Range of Oregon, *P. albipes* was captured in all five types. Based on captures per unit effort (number/trap-night), however, *P. albipes* was most abundant in deciduous forest (0.89) followed in order by conifer-shrub (0.79), sapling-pole conifer (0.69), oldgrowth conifer forest (0.35), and sawtimber conifer forest (0.20—Gomez, 1992). Although widely distributed in the sere, *P. albipes* was captured 5.3 times more frequently in riparian zones (25 m from streamside) than upslope (200 m from streamside). In a multivariate analysis of habitat characteristics of species captured, *P. albipes* and *Clethrionomys californicus* exhibited opposite correlations and almost no overlap in capture localities suggesting some competitive exclusion (Gomez, 1992).

Based on examination of the contents of stomachs of three specimens from California, Howell (1928) suggested that *P. albipes* might be a food specialist whose diet was limited to roots of some plant. From stomach contents and colonic fecal pellets from 21 *P. albipes* collected in western Oregon, however, Voth et al. (1983) identified fragments of epidermis from leaves of at least 33 species in 23 families of plants. Leaves of four species of deciduous trees (mostly *Alnus rubra* and *Salix lasiandra*) composed 57% of the fragments identified, 15% was from eight species of shrubs (mostly *Berberis nervosa* and *Rubus parviflorus*), 23% from 15 species of forbs (mostly *Trifolium repens* and *Senecio sylvaticus*), and the remainder from pteridophytes and grasses. Forbs, shrubs, and deciduous trees contributed to the diet throughout the year, but the contribution of forbs was greatest in early spring, that of deciduous trees greatest in summer and autumn, and that of shrubs greatest in autumn and winter. Other materials identified among the ingesta were moss gametophytes and pollen grains, and hair shafts and exoskeletons presumably from parasites obtained during grooming. No particles of seeds, fruits, fungi, or animals were found.

Because voles that had eaten leaves of deciduous trees were taken before leaf fall, Voth et al. (1983) concluded that the white-footed vole foraged arboreally. Nevertheless, they were quick to emphasize that the presence of low forbs and grasses in the diet and the fact that these voles are caught in traps set on the ground indicates that *P. albipes* is less arboreal than its congener *P. longicaudus*. Also, the presumed association of *P. albipes* with small streams might be related to its foraging on riparian and forest species rather than on aquatic or semi-aquatic vegetation (Voth et al., 1983). Voth et al. (1983:6) indicated that *P. albipes* and *P. longicaudus* were "among the smallest browsing arboreal mammals known." *P. albipes* has been maintained in captivity for more than a month on a diet of leaves and stems of Pacific blackberry (*Rubus ursinus*—R. Hoyer, pers. comm., 7 June 1993).

Mammal associates of *P. albipes* include *Aplodontia rufa*, *Peromyscus maniculatus*, *Neotoma cinerea*, *Microtus oregoni*, *M. longicaudus*, *M. townsendii*, *Clethrionomys californicus*, *Zapus trinotatus*, *Tamias townsendii*, *Sorex pacificus*, *S. trowbridgii*, *S. vagrans*, *S. bendirii*, *Scapanus orarius*, *S. townsendii*, *Neotrichogale gibbsii*, *Sylvilagus bachmani*, *Mustela erminea*, and *Spilogale gracilis* (Jewett, 1920; Gomez, 1992; Maser and Hooven, 1969). Potential predators include "owls, weasels, mink, spotted skunks, and domestic cats (Maser et al., 1981:201).

Parasites known to infest *P. albipes* include the fleas (Siphonaptera): *Catallagia s. sculleni*, *Epitedia scapani*, *Hystrichopsylla o. occidentalis*, *Megabothris abantis*, and *Rhadinopsylla sectilis goodi* (Lewis et al., 1988). Seemingly, there are no records for endoparasites or other groups of ectoparasites for the species.

Many published accounts record the collection of only a few *P. albipes* at a site. Whether this represents low density, arboreality, lack of attractiveness of baits, avoidance of traps by some individuals, some unknown behavior, or a combination thereof is unknown. Although *P. albipes* has been captured in a variety of traps, type of trap used may be responsible for observed differences in capture rates among some recent intensive studies. In 40,152 trap-nights with live traps at two sites each in oldgrowth and mature coniferous forest in the central Cascade Range of Oregon, *P. albipes* was not among the 19 species captured (Doyle, 1986); in 10,800 trap-nights, Anthony et al. (1987) caught one in oldgrowth and two in mature forests in museum special or rat traps on streamside transects in the same region; in 31,200 trap-nights, McComb et al. (1993) caught 10 at streamside and one upslope in pitfalls and museum special traps set in six mature (120–140 years old) stands in the Coast Range; and in 100,800 trap-nights in the same region, Gomez (1992) caught 59 in pitfalls set in five different-aged communities.

Maser and Johnson (1967:24) declared the species "the rarest microtine rodent in North America" (later modified to "one of the rarest microtine rodents north of Mexico"—Voth et al., 1983:1). Nevertheless, there has been a continuing increase in the number of specimens available for study. In the 29 years after the first specimen was taken in 1899 (Merriam, 1901), the number of specimens known increased to 15 (Howell, 1928); in the next 39 years, the number increased to 28 (Maser and Johnson, 1967); in the following 5 years, the number expanded to 45 (Olterman and Verts, 1972), and increased to 61 during the next 10 years (Johnson and Maser, 1982). In 1983–1991, 73 additional specimens reportedly were caught (Anthony et al., 1987; Gomez, 1992; McComb et al., 1993); however, not all of these specimens have been deposited in museums.

The species was considered "rare" by Olterman and Verts (1972:17) in Oregon, but they emphasized that several researchers had indicated that it may "be shown to be more common than is presently believed." The paucity of specimens in systematics collections may not be indicative of a rarity of *P. albipes* in nature, because its largely folivorous diet and its partly arboreal habit may reduce its vulnerability to being caught in traps commonly baited with rolled oats and peanut butter and set at ground level. Nevertheless, despite possessing some *r*-selected attributes (having relatively low body mass at birth and occupying early seral communities), the small average litter size (considered diagnostic of *K*-selected species) in comparison with other arvicoline rodents (Nadeau, 1985) suggests that *P. albipes* is a fairly strong *K*-strategist for an arvicoline.

GENETICS. Based on a personal communication from T. C. Hsu, the karyotype of *P. albipes* was reported as "similar but not identical" with that of *P. longicaudus* and that of *P. longicaudus* as "quite different" from that of *P. intermedius* (Johnson and Maser, 1982:19). No description of the karyotype was provided.

REMARKS. *Phenacomys albipes* is classified as a sensitive species by the Oregon Department of Fish and Wildlife (Marshall, 1992) and as a species of special concern by the California Department of Fish and Game. It currently is classified as a category 2 candidate species for which some information indicates that it may be appropriate to be listed under the Endangered Species Act (A. Pfister, pers. comm., 14 February 1994).

The generic name *Phenacomys* was derived from the Greek prefix *phenax* meaning "a cheat or imposter" and the Greek *mys* meaning "mouse" (Jaeger, 1978:160, 193). The specific name *albipes* was derived from the Latin *albus* meaning "white" and the Latin *pedalis* meaning "of or belonging to the foot" (Jaeger, 1978:12, 185).

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